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Genetic and epigenetic regulation of phenotypic variation in invasive plants – linking research trends towards a unified framework

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Abstract

Phenotypic variation in the introduced range of an invasive species can be modified by genetic variation, environmental conditions and their interaction, as well as stochastic events like genetic drift. Recent studies found that epigenetic modifications may also contribute to phenotypic variation being independent of genetic changes. Despite gaining profound ecological insights from empirical studies, understanding the relative contributions of these molecular mechanisms behind phenotypic variation has received little attention for invasive plant species in particular.

This review therefore aimed at summarizing and synthesizing information on the genetic and epigenetic basis of phenotypic variation of alien invasive plants in the introduced range and their evolutionary consequences. Transgenerational inheritance of epigenetic modifications was highlighted focusing on its influence on microevolution of the invasive plant species. We presented a comprehensive account of epigenetic regulation of phenotypic variation and its role in plant invasion in the presence of reduced standing genetic variation, inbreeding depression and associated genomic events which have often been observed during introduction and range expansion of an invasive alien species. Finally, taking clues from the studies conducted so far, we proposed a unified framework of future experimental approaches to understand ecological and evolutionary aspects of phenotypic variation. This holistic approach, being aligned to the invasion process in particular (introduction-establishment-spread), was intended to understand the molecular mechanisms of phenotypic variation of an invasive species in its introduced range and to disentangle the effects of standing genetic variation and epigenetic regulation of phenotypic variation.

Keywords

epigenetics, evolution, genetic diversity, phenotypic variation, plant invasion, transgenerational inheritance

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Introduction

With the increasing number of reports on negative impacts of invasive species on regional biota (Bellard et al. 2017; Early et al. 2016; Iacarella et al. 2015), biological invasion has become a severe problem globally and for obvious reasons, is in the spotlight of recent research trends. Numerous studies have been conducted to identify how a minor component of native communities has successfully established itself in a new and heterogeneous environment and becomes dominant in the invaded communities (Callaway and Maron 2006).

Multiple hypotheses have been put forward to explain successful invasion, e.g. resource fluctuation, enemy release hypothesis, evolution of increased competitive ability (EICA) [reviewed by (Catford et al. 2009; Inderjit et al. 2005)]. Among these, the influence of genetic diversity on invasion success has been long recognized (Baker and Stebbins 1965) and numerous studies have been conducted to explain this relationship [e.g. (Facon et al. 2006; Lavergne and Molofsky 2007; Roman and Darling 2007)]. Standing genetic variation can result in rapid selection of population showing greater fitness leading to successful establishment and range expansion of the introduced species (Barrett 2015; Sakai et al. 2001). On the other hand, introduction in a new location and range expansion from the point of introduction may cause population size reduction (demographic bottleneck) which can reduce genetic variation (Estoup et al. 2016; Uller and Leimu 2011), and subsequently may lead to inbreeding and considerable loss of fitness (Schrieber and Lachmuth 2017). However, even genetically depleted founder populations may establish and spread successfully if:

i) detrimental inbreeding effects are mitigated (Hufbauer et al. 2013; Rosche et al. 2017; Schrieber and Lachmuth 2017) by one or several of preventive mechanisms like multiple introductions [(Dlugosch and Parker 2008a; Uller and Leimu 2011); but see Hagenblad et al. 2015], genetic admixture among introductions (Roman and Darling 2007), preadaptation to the environment found in the introduced range (Hufbauer et al. 2012), and polyploidy (Pérez et al. 2006), or
ii) the plasticity of ecologically relevant traits of a genotype is enhanced in a way it can take advantage of a wider ecological niche (Bossdorf et al. 2008; Muth and Pigliucci 2007; Richards 2006; Spens and Douhovnikoff 2016; Walls 2010). Evolutionary changes in traits related to log-distance dispersal, growth rate, tolerance to environmental heterogeneity, and competitive ability in response to novel environmental conditions have been found to promote invasiveness (Bhattarai et al. 2017; Davidson et al. 2011; van Kleunen et al. 2010).

Epigenetic modifications in gene expression, being independent of any changes in DNA sequence (Nicotra et al. 2010; Richards 2006; 2011; Scoville et al. 2011), have been recognized as key mechanisms behind the expression of inbreeding depression (Biémont 2010; Nebert et al. 2010; Vergeer et al. 2012) and plastic responses of plant traits to environmental cues (Herrera and Bazaga 2013). Epigenetic changes can be

induced by environmental stresses, both biotic and abiotic [e.g. (Dowen et al. 2012; Verhoeven et al. 2010)], and invasive plants are frequently exposed to these interactions in their introduced environment (Blackburn et al. 2011; Nunez-Mir et al. 2017; Zefferman et al. 2015). However, while there has been some progress in epigenetic studies in model and non-model organisms, studies with invasive plants have so far been limited to reviewing broad patterns of epigenetic variation (Richards et al. 2017). Moreover, it has been found that adaptive evolution to local conditions, phenotypic plasticity, or sometimes a combination of both, help invasive species to compete in a range of environments (Liao et al. 2016; Montesinos and Callaway 2018). Experimental studies on local adaptation and phenotypic plasticity are often conducted separately (but see Liao et al. 2016), thereby leaving a gap in comprehensive understanding of relative contribution of genetic differentiation and epigenetically regulated phenotypic variation on invasion success.

In this context, a comprehensive appraisal of the role of genetic and epigenetic variation in plant invasion and future prospects for investigation appears to be timely. This review was therefore framed to i) recognize the factors responsible for phenotypic variation; ii) identify the role of epigenetic processes in maintaining fitness of invasive plants; and iii) to propose a unified framework of experimental approaches to understand the relative importance of genetic differentiation and epigenetic regulation of trait fitness.

Factors responsible for phenotypic variation in the introduced range

Genetic basis of phenotypic variation

In the first step of the invasion process, a species can be introduced from its native range either by introduction of a few or even only a single genotype or through multiple introductions from different source populations of its native range. Multiple introductions of the species may give rise to two situations: i) the introduced genotype(s) can be restricted within the introduced region(s) and/or ii) multiple introductions from different source populations, breaching of geographical barriers, intra- or interspecific hybridization may produce genetically diverse populations and different phenotypes (phenotypic divergence). Phenotypic variation among the introduced populations is therefore dependent on the number of introduced genotypes (standing genetic variation) and can be increased by intra- and inter-specific hybridization. In addition to standing genetic variation, new mutations may also contribute to phenotypic variation (Fierst 2011; Lambertini et al. 2010). Recent studies found that a variety of mutation types occur frequently in the founding populations and these structural as well as regulatory mutations can have large effects on phenotype (Dlugosch et al. 2015). Given the short time frame for the introduced populations to respond to selection forces, standing genetic variation may contribute largely for adaptive evolution (Prentis et al. 2008). However, the arrival of new mutations may also provide scopes of selection of traits at low effective population sizes during range expansion of introduced

species (Dlugosch et al. 2015). Moreover, phenotypic divergence in the introduced range often occurs under non-equilibrium demographic conditions and is frequently affected by prior evolutionary history in native range and stochastic events (e.g. genetic drift) (Keller and Taylor 2008). Natural selection can, therefore, act in native as well as in invasive range or during establishment in the invasive range (adaptive divergence).

Epigenetic basis of phenotypic variation

In addition to genetic-differentiation driven phenotypic divergence among the introduced populations, an individual genotype may also produce phenotypic variation in response to different environmental conditions of the introduced range (phenotypic plasticity). Epigenetic changes (without any change in DNA sequence) can contribute to phenotypic variation in plant traits independently of genetic variation (Richards et al. 2012). Therefore, while in the case of genetically diverse populations, both local adaptation and phenotypic plasticity may contribute to successful establishment of an invasive species in a novel environment, epigenetically regulated phenotypic variation may be responsible for the establishment of an invasive population in the absence of genetic variation. Epigenetic responses are caused by reversible enzyme mediated modifications of DNA, associated histones, and the generation of regulatory small non-coding RNA molecules leading to controlled transcriptional activity of genes, repetitive sequences and transposable elements (TEs) (Pikaard and Mittelsten Scheid 2014). These epigenetic variations can be induced by several developmental signals and environmental stresses (Chinnusamy and Zhu 2009). One of the best studied epigenetic mechanisms to date in plants is DNA methylation in which a methyl group is added to one of the four bases (usually cytosine) in the DNA molecule (Finnegan et al. 1998). Cytosine methylation occurs in CG, CHG and CHH contexts, where H = Adenine (A), Cytosine (C) or Thymine (T) nucleotides, and the reaction is catalyzed by methyltransferase enzyme. DNA methylation is enzymatically reversible by the action of DNA glycosylase enzymes.

Several studies have been conducted on model and non-model species, both in field and controlled conditions to quantify epigenetic influence on trait variation being independent of genetic variation (Abratowska et al. 2012; Latzel et al. 2013; Wu et al. 2013). For example, in a controlled greenhouse study and reciprocal transplant experiment, genetic and epigenetic diversity were compared across 16 populations of Japanese knotweed (*Fallopia japonica*) from three habitat types of its invaded range in USA (Richards et al. 2012). This study found higher epigenetic variation across habitat types, response of some epigenetic loci to local microhabitat conditions and low genetic diversity across populations. Comparing populations of *Poa annua* from its Antarctic (introduced) and Polish (native) ranges, Chwedorzewska and Bednarek (2012) found lower genetic differentiation but increased epigenetic variation in the introduced range compared to the native populations. These evidences indicated that epigenetic variation can contribute to phenotypic variation in plant traits independently of genetic

variation. Epigenetic variation can be operational even on a short time scale as evident from a study on an invasive plant *Alternanthera philoxeroides*. Epigenetic variation in morphological traits of this invasive plant was examined in two habitats (aquatic and terrestrial), first in natural condition followed by common garden experiments (Gao et al. 2010). Considerable DNA methylation polymorphisms were observed within and between natural populations. Reciprocal transplantation of the ramets from the source populations induced morphological changes and epigenetic reprogramming, thereby indicating reversible induction of DNA methylation in a short period of time.

In addition to environmentally induced epigenetic variation, spontaneous epimutation may also cause the observed epigenetic differences among natural population. For example, a multi-generation common garden experiment on *Alternanthera philoxeroides* revealed that a combination of environmental induction and spontaneous epimutation resulted in epigenetic variation in the species (Shi et al. 2019). These epigenetic variations, either induced environmentally or resulting from spontaneous epimutation or both, may be stably inherited across generations (Jablonka and Raz 2009). This phenomenon is usually termed as transgenerational epigenetic inheritance and in plants, this process depends on a methyltransferase enzyme that replicates methylation patterns during both mitosis and meiosis (Takeda and Paszkowski 2006). In case of sexual reproduction, either meiotic resetting of epigenetic variation may occur or the epigenetic changes may bypass the surveillance mechanisms and are transmitted to the next generation. In clonal propagation, epigenetic changes are more stably inherited to the progeny since it is assumed that meiosis does not occur in vegetative reproduction. These heritable epigenetic modifications provide a platform for natural selection to act on ecologically relevant traits (Prentis et al. 2008), thereby contributing to the microevolution of natural populations (Bossdorf et al. 2008; Richards et al. 2017). Two mechanisms have been proposed to explain the role of epigenetic modifications in the evolution of natural populations.

First, similar to genetic variation, heritable epigenetic variation may translate into phenotypic variation and fitness differences among individuals for natural selection to act on. On the other hand, unlike genetic variation, epigenetic variation is altered by environmental conditions directly and, therefore, may provide an additional, accelerated way for evolution (Bossdorf et al. 2008). For example, population genomic analysis of three climatologically distinct *Quercus lobata* populations (Platt et al. 2015) revealed that DNA methylation (specifically, CpG methyl polymorphisms) was involved in local adaptation, either directly or through linkage to regions under selection.

Secondly, epigenetic mechanisms play a role in adaptive transgenerational plasticity, defined as the ability of the parent population to alter traits in their offspring which may enhance their fitness in similar environmental conditions (Galloway and Etterson 2007). Unlike mammals in which resetting of DNA methylation takes place during early embryonic development (Santos et al. 2002), the epigenetically induced phenotypic changes in plants can be inherited over several generations (Bräutigam et al. 2013) and thus give rise to epialleles (Jablonka and Raz 2009; Schulz et al. 2014). Epialleles can be defined as the forms of a gene that are responsible for heritable phe-

notypic variation without changing DNA sequence (Quadrana and Colot 2016). The best studied examples so far highlight the inheritance of induced epigenetic effects to the unstressed progeny of parents exposed to biotic and abiotic stresses (reviewed by (Holeski et al. 2012)). For example, in an experiment with multiple genetic lines of annual *Polygonum persicaria*, parental plants were grown in dry (drought-stressed) versus moist (well-watered) soil and their offspring were exposed to a demethylating agent zebularine during seed germination (Herman and Sultan 2016). Under controlled conditions (without zebularine treatment), the offspring of dry soil grown (drought-stressed) parental population produced longer root systems and more biomass in comparison to the offspring of moist soil grown parental population. Treatment with zebularine removed these developmental effects from the offspring of drought-stressed parents, while the offspring of well-watered parents showed non-significant alteration of phenotypic expression. These findings provide empirical evidence of epigenetic contribution to adaptive transgenerational plasticity from stressed parental population to offspring. However, the magnitude of epigenetic changes and their heritability may vary depending on the environmental conditions. For example, genetically identical apomictic *Taraxacum officinale* plants were exposed to different ecological stresses (salt, nutrient, chemicals mimicking herbivore and pathogen attacks) and the progeny of the stressed plants were raised in a common unstressed environment (Verhoeven et al. 2010). The study revealed heritability of induced changes; however, the variation in methylation pattern was noted among different stresses.

While most of the molecular investigations on transgenerational inheritance of epigenetic changes have been restricted to model and endemic species (Hauser et al. 2011; Henderson and Jacobsen 2007), evidences are rare for invasive plants which have been frequently exposed to biotic and abiotic stresses in the introduced environment. Exceptions exist, for example, in case of invasive *Fallopia* spp. (Japanese knotweed), Richards et al. (2012) observed epigenetic variation in leaves of the progeny plants after growing the rhizomes (collected from different habitats, *i.e.* across an abiotic stress gradient) in a common environment. This multigenerational experiment showed that parental exposure to abiotic stresses resulted in modified DNA-methylation in unexposed offspring.

Role of epigenetic processes in plant invasion

Genetic adaptation paradox and epigenetic regulation of phenotypic variation

After successful introduction (*i.e.* crossing the geographic and cultivation barriers, (Blackburn et al. 2011), some alien plant species establish wild populations in novel habitats. Two hypotheses, namely the ecotype hypothesis and the plasticity hypothesis, have been proposed for invasive plants to explain this ability of habitat accommodation (Geng et al. 2007). The ecotype hypothesis suggests that genetically based variations leading to local adaptation are responsible for thriving across different habitats. The positive relationship between genetic diversity of the founder population and invasion

success (in terms of higher population growth rates and higher adaptability and dispersal ability) has been well-established (Bock et al. 2015; Collins et al. 2018; Crawford and Whitney 2010). A meta-analysis of differences in the frequency and magnitude of local adaptation between 47 alien invasives and 91 native species showed that local adaptation in invasive plant species was frequent and comparable to that exhibited by native plant species (Oduor et al. 2016).

However, contrasting examples also exist where introduced plant populations with very low genetic diversity (and lower in comparison to native populations) have been found to be successful invaders (Hagenblad et al. 2015; Ren et al. 2005; Zimmermann et al. 2010). For example, a global scale population genetic survey using amplified fragment length polymorphism (AFLP) markers of the aquatic invader *Eichhornia crassipes* (water hyacinth) revealed very low genetic diversity in the introduced populations, 80% of which were composed of a single clone leading to little differentiation compared with those from the native range (Zhang et al. 2010). In a recent study on invasive *Fallopia* (Japanese knotweed) in Norway (northerly distribution range in Europe), no genetic variation was observed within this invasive taxon (Holm et al. 2017).

Populations with such restricted genetic variation may find other mechanisms to extend the ability of a single genotype, or general-purpose genotype or GPG (Baker 1965), to take advantage of a wider ecological niche (Spens and Douhovnikoff 2016). This paradox of invasion success of the introduced populations in spite of having low genetic diversity has been attributed to phenotypic plasticity of traits (plasticity hypothesis) (Bossdorf et al. 2005). Phenotypic plasticity is considered as one of the underlying mechanisms of general purpose genotype (GPG) model (Massicotte and Angers 2012) and is more important in rapidly fluctuating habitats (Clements and Ditommaso 2011). Many studies have highlighted the role of phenotypic plasticity on the successful invasion of exotic plant species (Hagenblad et al. 2015; van Kleunen et al. 2010), mostly for clonal species for which local adaptation is usually not observed (Geng et al. 2016). Clones of an invasive species *Alternanthera philoxeroides* showed varying levels of genetic diversity (in terms of both ISSR marker diversity and quantitative trait variation) between and within its native range (Argentina) and two invasive ranges - China and the USA (Geng et al. 2016). However, significant phenotypic plasticity in biomass allocation and morphological traits in response to varying water availability was observed in all clones regardless of their geographic origins, suggesting the possible role of phenotypic plasticity to invade diverse habitats across broad geographic areas. In addition, adaptive transgenerational plasticity contributes to the exotic species growth and successful establishment in a novel environment (Campbell et al. 2015; Dyer et al. 2010; Fenesi et al. 2014) and natural selection for particular traits may promote range expansion directly (Clements and Ditommaso 2011). For example, despite the loss of genetic variability in the invaded range, *Hypericum canariense* was found to be a successful invader in the Hawaiian Islands, San Diego and Calfornia, USA, and substantial adaptive evolution in growth rate and flowering phenology was found to overcome this genetic depletion (Dlugosch and Parker 2008b). Epigenetic modifications in gene expression and function have been recognized as key mechanisms behind phenotypic variation of plant traits in response to such environmental cues (Herrera and Bazaga 2013).

The potential role of epigenetics in the expression of inbreeding depression in founder populations

Reduced genetic diversity during invasions may not only result in a loss of adaptive potential; it may also increase inbreeding rates. Inbreeding enhances the phenotypic expression of deleterious recessive mutations leading to a loss of fitness in the offspring generation (*i.e.*, inbreeding depression), which can considerably hamper invasion success (Schrieber and Lachmuth 2017). Inbreeding depression is found more commonly in stressful environments (Reed et al. 2012) and multiple studies have been conducted to establish this synergistic relationship between inbreeding and environmental stress (e.g. (Campbell et al. 2013; Kariyat et al. 2012; Kristensen et al. 2010). Recent empirical studies support that inbreeding x environment interactions can prevent or foster successful invasion (Hufbauer et al. 2013; Rosche et al. 2017; Schrieber et al. 2019), while molecular studies suggest that epigenetic modifications play a decisive role in stress responses (Chinnusamy and Zhu 2009) and the expression of inbreeding depression. For example, a study on *Scabiosa columbaria* (a self-compatible but predominantly outcrossing species) revealed that inbreeding caused inbreeding depression for fitness-related traits and increased methylation levels (Vergeer et al. 2012). This study observed elimination of inbreeding depression by restoring the increased DNA methylation level in inbreds to the outbred level and concluded that DNA methylation could mediate the negative effects of inbreeding. In summary, these studies suggest that epigenetic changes may be involved in purging (i.e. recovery from inbreeding depression) (Nebert et al. 2010). However, to the best of our knowledge, empirical evidence on the relationship between epigenetic modifications and inbreeding depression in invasive plants is lacking. We require more basic knowledge on the role of epigenetics in the expression of inbreeding depression from the field of genetics and molecular biology before we can apply and test this concept in the context of plant invasions.

Epigenetic alterations associated with genomic events during plant invasions

Epigenetic modifications may not only contribute to establishing the success of genetically depleted plant founder populations, but they may also further enhance the adaptive potential of intra-or inter-specifically hybridized or polyploid invaders. Genomic events such as intra-or inter-specific hybridization between genetically distinct source populations and polyploid formation are responsible largely for speciation (Rapp and Wendel 2005) and increasing the evolutionary potential of invasive species (Rius and Darling 2014; van Kleunen et al. 2015) leading to successful invasion (Ellstrand and Schierenbeck 2000). Multiple introductions and intraspecific hybridization have been found to lead to the increase (or retention of) genetic diversity, and subsequently fitness of the invading population like *Bromus tectorum* (Novak and Mack 2005), *Phalaris arundinacea* (Lavergne and Molofsky 2007), *Senecio pterophorus* (Vilatersana et al. 2016), *Ambrosia artemisiifolia* (van Boheemen et al. 2017).

During these processes of intra-or inter-specific hybridization and allopolyploid formation, epigenetic alterations are found to be prevalent (Rapp and Wendel 2005). A classic example of epigenetic modification during intraspecific hybridization and its role in invasion success has been found in a series of studies involving the genus *Spartina* (Aïnouche et al. 2009; Parisod et al. 2009; Salmon et al. 2005). In these experiments, methylation repatterning was observed in two hybrid species (*Spartina* x *townsendii* and *Spartina* x *neyrautii*), although these hybrids were genetically uniform with their ancestors (American introduced *Spartina alterniflora* and European native *Spartina maritima*) (Salmon et al. 2005). These studies also identified intraspecific hybridization as a primary stimulus in the invasion success of polyploid *Spartina* species (Aïnouche et al. 2009). However, the connections between these epigenetic alterations and morphological or ecological phenotypes of the hybrids are yet to be discovered (Rapp and Wendel 2005). Nevertheless, genomic events (e.g. intra-or inter-specific hybridization, polyploidization) inducing epigenetic changes leading to morphological variation has been reported from various model plant systems, e.g. in allopolyploid *Brassica rapa* (diploid *Brassica napus* x *Brassica oleracea*) (Rapp and Wendel 2005). It is interesting to note that epigenetic modifications could vary between different groups of plants, and even between ploidy levels. For example, MS-AFLP analysis in synthetic *Gossypium* (cotton) tetraploids and hexaploids showed different methylation pattern in comparison to their diploid and tetraploid progenitors (Liu et al. 2001).

Towards a unifying research framework

One of the major objectives of this review has been finding a comprehensive structural guideline of experimental approaches taking clues from the studies already conducted on invasive and non-invasive, model and non-model species. Phenotypic variation in a plant species in its introduced range is one of the most highly-researched topics in invasion biology in which basic ecological research demonstrated the role of phenotypic variation in the invasion success of exotic species. On the other hand, genetic variation, microevolution and epigenetic processes have been found to play significant roles in the phenotypic variation of traits, and therefore, have been recognized as relevant to understand the mechanisms underlying the natural variation in ecologically important traits (e.g. Colautti and Barrett 2013; Liao et al. 2016; Marchini et al. 2019; Oduor et al. 2016). In this context, a bridge between these parallel but complementary experimental approaches may provide a comprehensive understanding of ecological and evolutionary aspects of phenotypic variation of traits and their roles in the invasion process (introduction-establishment-spread continuum). This empirical framework is, therefore, specifically aimed to broaden the scope of research by including the genetic investigation components into the ecological studies on the phenotypic variation of traits in the invasive species. For this purpose, a model system has been conceptualized based on an invasive plant species which has been reported to have i) phenotypic variation across environmental gradients, and ii) reproduction ability through both sexual

and vegetative means. We first aligned the proposed framework with three different stages of invasion (introduction, establishment and spread) to identify the possible locations where genetic differentiation and/or epigenetic regulation can act (Figure 1). We proposed future experimental studies (Figure 2) to understand the relative importance of genetic and epigenetic regulation of trait fitness along the course of the invasion process. The methodologies usually adopted for these experiments have been given in Table 2 with their respective strengths and challenges while detailed methodologies for screening epigenetic variation in invasive plants have been provided in Box 1.

Field and controlled experiments are being conducted to characterize phenotypic variation of invading populations, often in comparison to their native congeners and to other species native to the invaded habitat (van Kleunen et al. 2010). Reciprocal transplant and/or common garden experiments are suitable for delineating the effects of local adaptation and phenotypic plasticity on successful invasion of an exotic species (Figure 2). In reciprocal transplant experiments, individuals from different populations are transplanted between the original habitats from where the populations were sampled and population x test habitat interactions are quantified in terms of fitness parameters (Kawecki and Ebert 2004). The alternative approach to this involves creating the properties of different habitats in greenhouse or experimental plots, where fitness functions of different populations have been quantified. This experimental set-up is known as common garden (explant) studies. In a common garden experiment, two or more populations of a species growing in their native and non-native environments are transplanted in a common environment so that the genetic basis of the observed differences among field populations can be identified (Molofsky et al. 2017; Parker et al. 2003). While in field experiments (marked '1' in Figure 2), identifying plastic responses to a set of well-defined stress factors is important for comparative studies (Gratani 2014), manipulation of resource conditions in a biologically meaningful manner is required in reciprocal transplant and/or common garden studies (marked '2.1' in Figure 2) to yield important and relevant information (Davidson et al. 2011). In a reciprocal transplant experiment, plants from different invasive populations can be grown in a common environment to compare fitness traits. Higher mean fitness for all the traits of the local population compared to foreign population will indicate local adaptation (Local versus Foreign comparison). Significant difference in trait values among transplant sites (for a population) will indicate plastic responses whereas difference among populations (for a site) will indicate genetic differentiation. However, this approach is often confounded by intrinsic issues of population quality, e.g., inbreeding and transgenerational effects (Blanquart et al. 2013). The average effects of transplantation can be measured by comparing trait values between the local site and all away sites (Sympatric versus Allopatric comparison); however, this approach has been also found to be confounded by strong local advantage.

For example, morphological differentiation was studied between weedy, non-native and non-weedy, native populations of *Centaurea solstitialis* in a common garden setting and further compared using neutral genetic variation at simple sequence repeat markers (Eriksen et al. 2012). This study found quantitative variation to be more strongly partitioned among regions than genetic variation, which suggests that local adaptation

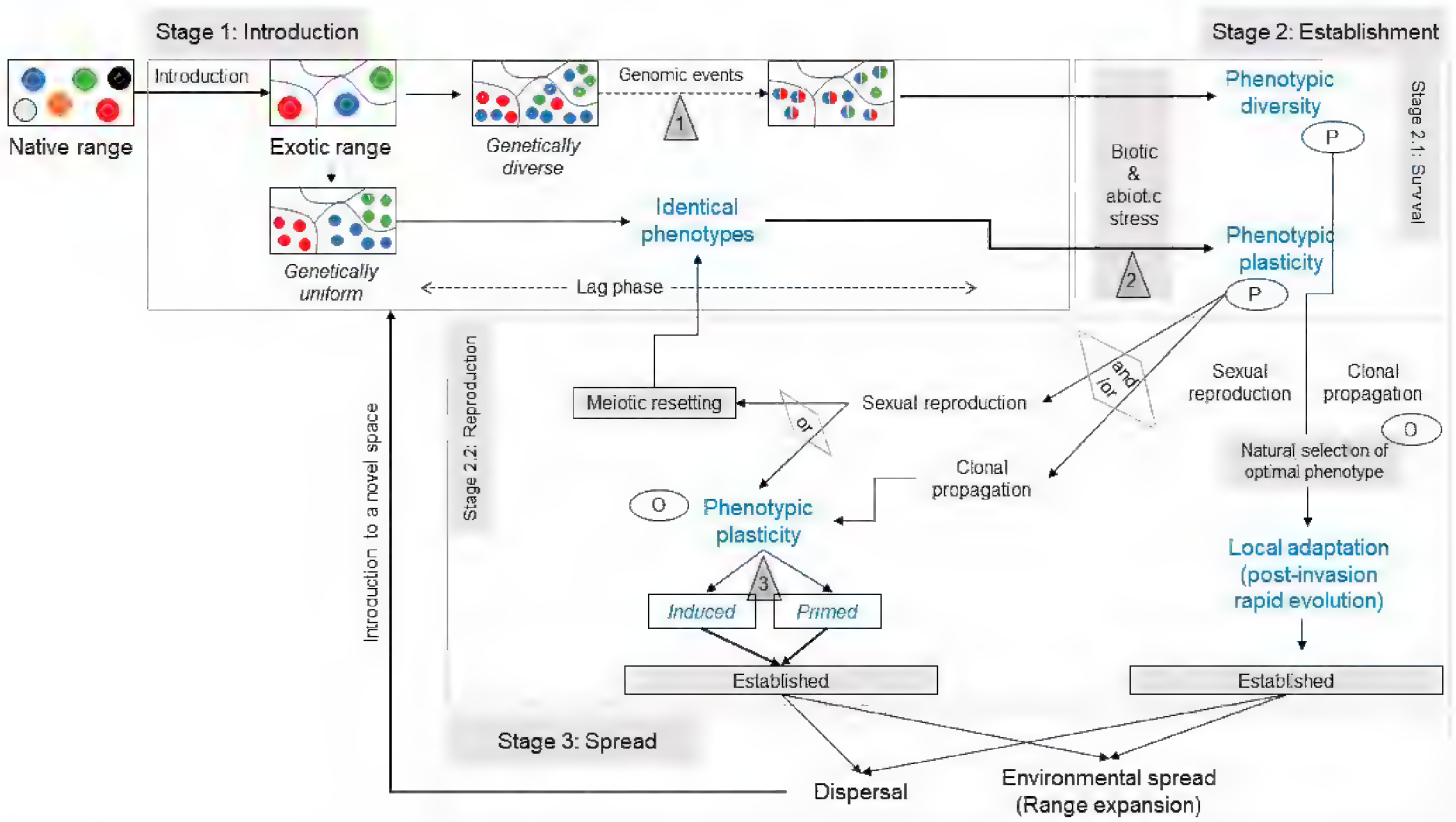

Figure 1. Conceptual framework for differentiating genetic and epigenetic basis for phenotypic variations across three stages of alien plant invasion process (introduction, establishment, spread). While genetic differentiation between introduced populations may cause phenotypic variation which leads to local adaptation and post-invasion rapid evolution through selection of traits and natural selection of optimal phenotype across environmental conditions, epigenetically regulated phenotypic variations are more prevalent in genetically similar populations. Three sites where epigenetic mechanisms may influence invasion success have been marked with triangles: 1) in case of genetic admixture between different genotypes present in a region, 2) biotic and abiotic stress induced epigenetic alterations among the genetically similar populations, and 3) transmission of epigenetic information from the parents (P) to the offspring (O) making the progeny capable of dealing with similar kinds of parental environment.

might play a role in successful invasion of the species. In a recent transplantation experiment, local adaptation and phenotypic plasticity were examined in terms of fitness responses for sexual and clonal reproductive measures and vegetative responses of an invasive plant *Fallopia japonica* across a broad latitudinal range within North America (van Wallendael et al. 2018). This study reported significant effects of the source population (suggesting genetic differentiation) and transplant sites (suggesting phenotypic plasticity) for all vegetative traits, but no evidence of local adaptation was found for sexual or clonal reproductive traits. Contrasting examples are also found in which phenotypic plasticity can be operational being independent of genetic variation. For example, trait plasticity and genetic variation were examined across 16 populations of Crofton weed (*Eupatorium adenophorum*) in China in a common garden experiment followed by intersimple sequence repeat (ISSR) marker analysis. This study revealed the presence of high phenotypic plasticity of functional traits despite having low genetically based variation (Zhao et al. 2012).

However, phenotypic differentiation in invading populations may also arise from random shifts in allele frequencies during repeated demographic disequilibrium (i.e.,

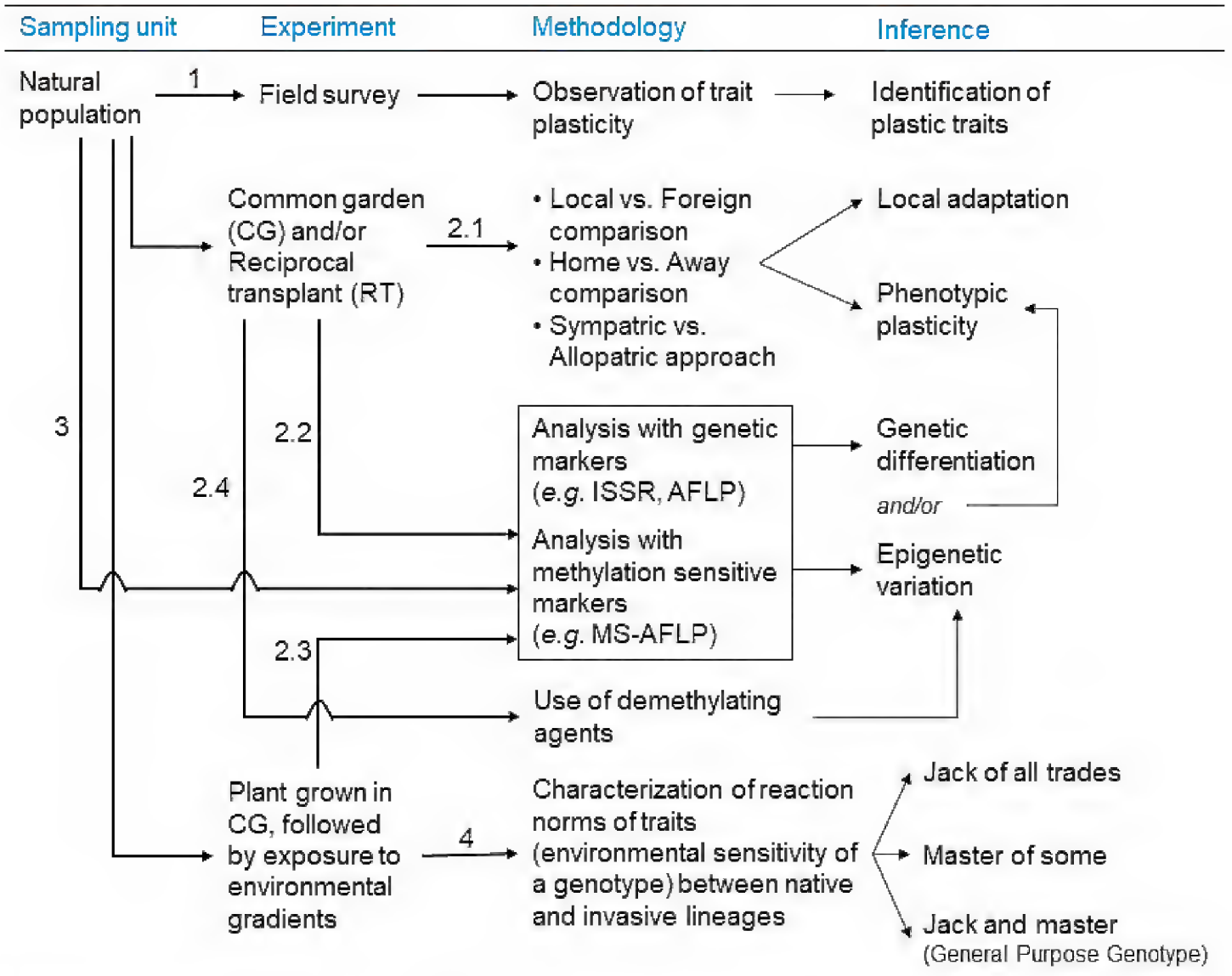

Figure 2. Experimental framework for differentiating genetic and epigenetic regulation of phenotypic plasticity. While a field survey of natural populations may identify plastic traits (1), reciprocal transplant experiments comparing performances of local and foreign populations may give insights into local adaptation, phenotypic plasticity and genetic differentiation as well (2.1). Plants grown in common garden experiments may be subjected to analysis with genetic and methylation-sensitive markers (2.2) or they can be exposed to environmental stresses before analysis (2.3) to identify genetic and epigenetic variation regulating trait plasticity. The use of demethylating agents (2.4) can also provide indirect evidence of transgenerational epigenetic inheritance. Samples from the natural population can also be analyzed with these markers followed by proper statistical analysis to disentangle genetic and epigenetic effects on trait plasticity (3). Characterization of reaction norms of the plants (e.g. comparison between native and invasive lineages) grown in common garden in response to environmental gradients (4) may highlight the trade-offs between maintaining a high performance across a range of conditions (robustness or jack of all trades) and maximizing fitness in an environmental condition (opportunism or master of some) or both (robust to environmental conditions and high performance, the general-purpose genotype).

genetic drift). Thus it is necessary to account for non-adaptive evolutionary change when investigating adaptive differentiation in invaders (Keller and Taylor 2008). In this context, information from neutral genetic markers can be used to control for, and quantify the effect of, non-adaptive processes with different statistical approaches (Agrawal et al. 2015; Keller et al. 2009; Meimberg et al. 2010; Schrieber et al. 2017). For example, genetic differentiation in phenotypic traits across environmental gradients was tested

Table 1. Examples of experimental studies investigating the role of epigenetic variation in phenotypic plasticity in both non-native and native, model and non-model species in controlled as well as field-based experiments. The factors which may influence the experimental designing and outcomes are mentioned here: species reproduction (sexual, vegetative, or both), plant material used, environmental gradient responsible for epigenetically controlled plastic changes and genetic as well as methylation sensitive genetic marker-based analysis (AFLP = Amplified Fragment Length Polymorphism; MS-AFLP/MSAP/met-AFLP = methylation sensitive AFLP).

Obs.	Name of the species	Species status	Species reproduction	Experimental design	Plant material	Environmental gradient	Methodology	Reference
1	*Fallopia* sp. (Japanese knotweed)	Invasive	Vegetative and sexual	Controlled	Rhizome – Leaf	Diverse habitats	AFLP and MS-AFLP	Richards et al. (2012)
2	*Poa annua*	Non-native	Sexual	Field based	Shoot	Comparison between native & invasive populations	AFLP and met-AFLP	Chwedorzewska and Bednarek (2012)
3	*Alternanthera philoxeroides*	Non-native	Vegetative	Field based Common garden	Leaf Plant	Habitat – Aquatic and terrestrial	AFLP and MSAP	Gao et al. (2010)
4	*Spartina* sp. (5 species – 2 parents, 2 hybrids and 1 allopolyploid	Non-native	Sexual	Controlled	Leaf	Allopolyploid speciation	AFLP and MSAP	Salmon et al. (2005)
5	*Phragmites australis*	Introduced invasive and native non-invasive subspecies	Facultative clonal	Field based	Leaf	Comparison between native & invasive subspecies	AFLP and MS-AFLP	Spens and Douhovnikoff (2016)
6	*Ageratina adenophora* (Crofton Weed)	Non-native	Sexual and vegetative	Controlled	Leaf	Cold tolerance	*ICE1* gene methylation	Xie et al. (2015)
7	*Taraxacum officinale*	Endemic	Apomictic	Controlled	Seed – Leaf	Nutrient, Salt, Pathogen attack	AFLP and MS-AFLP analysis	Verhoeven et al. (2010)
8	*Arabidopsis thaliana*	Model species		Controlled	Seed – Leaf		Demethylating agent 5-azacytidine	Bossdorf et al. (2010)
9	*Viola cazorlensis*	Endemic	Sexual	Field based	Leaf	Adaptive epigenetic variation	AFLP and MSAP	Herrera and Bazaga (2010)
10	*Viola elatior*	Endemic	Vegetative and sexual	Field based	Leaf	Light availability	AFLP and MSAP	Schulz et al. (2014)
11	*Betula ermanii*	Endemic	Sexual	Field based	Leaf	Habitat	AFLP and MS-AFLP	Wu et al. (2013)
12	*Armeria maritima*	Endemic	Obligatory outbreeding	Controlled	Seed – Leaf	Metal concentration	AFLP and met-AFLP	Abratowska et al. (2012)
13	*Ilex aquifolium*	Endemic	Sexual	Field based	Leaf – heterophylly	Herbivory	MSAP	Herrera and Bazaga (2013)
14	*Laguncularia racemose*	Mangrove-endemic	Vegetative and sexual	Field based	Leaf	Habitat	MSAP	Lira-Medeiros et al. (2010)
15	*Viola cazorlensis*	Endemic	Sexual	Field based (long term: 20 years)	Leaf	Herbivory	AFLP and MSAP	Herrera and Bazaga (2011)

Based on a literature search on Web of Science to find experimental studies conducted to establish relationship between epigenetic variation and phenotypic plasticity. We used the search phrase "("phenotypic plasticity" AND "plant") AND ("epigenetic") AND ("transgenerational plasticity") AND ("epigenetics" OR "methylation"). The search result yielded 30 papers from which the empirical studies have been summarized in this table. We also considered references cited in these papers and the experimental studies have been included in this table. The references of these studies have been cited in the literature section.

between native and introduced populations of two perennial plants *Silene vulgaris* and *S. latifolia* in a common garden experiment (Keller et al. 2009) using AFLP loci and statistically controlling neutral processes like colonization history, gene flow and genetic drift. The results revealed evidence of adaptive differentiation for some traits while the role of neutral processes governing phenotypic variation was also found for other traits.

To identify genetic and epigenetic regulation of phenotypic variation, the invasive populations of the common greenhouse environment can be subjected to analysis with genetic and methylation-sensitive markers (marked 2.2 in Figure 2) [e.g. Richards et al. (2012)]. The plants can be exposed to environmental stresses in common garden experimental set-up and stress-induced phenotypic variation can be analyzed using both genetic and methylation-sensitive markers (marked 2.3 in Figure 2) (2.3) (e.g. Verhoeven et al. 2010). Samples from natural populations can also be analyzed with these markers followed by proper statistical analysis to disentangle genetic and epigenetic effects on trait variation (3) (e.g. Herrera and Bazaga 2013). In addition, use of demethylating agents like 5-azacytidine and zebularine inhibits the enzyme methyltransferase activity of DNA demethylation and therefore natural epigenetic variation can be identified from responses of different natural populations to the treatment of these demethylating agents (marked 2.4 in Figure 2). Similar approaches have been found successful to identify genetic and epigenetic regulation of phenotypic variation in model and non-model species (Table 2). For example, a set of natural genotypes of the model species *Arabidopsis thaliana* was treated with demethylating agent 5-azacytidine, and the effect of reduced DNA methylation was identified as the main cause of the observed phenotypic changes of plant traits (Bossdorf et al. 2010). In another greenhouse experiment, individuals of six genotypes of a perennial grass species *Festuca rubra* were treated with 5-azacytidine and their performances were measured across different environmental conditions (Münzbergová et al. 2019). This study found interactive effect of demethylation with the environment and genotype, thereby suggesting that epigenetic variation can be influenced by both genetic structure and local environment.

Experiments involving multiple generations of the species may detect the heritability of plastic traits across generations (stage 2.2 in Figure 1). The progeny population can be grown from the seeds or the clonal fragments of the parental population in the common garden experiment, and trait variability can thereafter be analyzed using genetic and methylation-sensitive markers. Alternatively, demethylating agents can also be used to have indirect evidence of transgenerational epigenetic inheritance. While the majority of these studies have been conducted across sexual generations [(e.g. (Herman and Sultan 2016)), very few studies identify adaptive transgenerational effects in clonally reproducing plant species, although clonal reproduction is recognized as the main reproductive strategy for most plant species (Rendina González et al. 2018). For example, adaptive transgenerational effects in clonal offspring of *Trifolium repens* were tested after exposing parental generation to drought and herbivory stress (Rendina González et al. 2017). 5-azacytidine was used to decrease the global methylation level of DNA relative to control plants. The study found an increased number and size of offspring ramets (branches arising from the transplanted stolon) from the parents

Table 2. Experimental designs commonly used for investigating the effect of epigenetic variation on phenotypic plasticity and transgenerational pattern of epigenetic changes across generations. Strengths and challenges associated with each of these approaches have been mentioned.

Experimental design		Examples	Strengths	Challenges
Study system	**Study procedure**			
Natural population	1. Sampling from plant materials (leaf, shoot) of identical developmental stages across a disturbance gradient 2. Analysis with molecular markers and methylation sensitive restriction enzymes (Box 1) 3. Statistical analysis to identify epigenetic variation that is not explained by genetic variation	(Herrera and Bazaga 2013; Schulz et al. 2014)	1. Consider dynamic ecological factors that exist in wild populations (Spens and Douhovnikoff 2016) 2. Three-way relationship (environment x phenotypic plasticity x epigenetic changes) can be established	1. Cannot identify whether the observed differences reflect heritable variation or repeated introduction (Richards et al. 2017) 2. Challenging for sexually reproducing organisms in which genetic and epigenetic variation may be closely intertwined (Herrera and Bazaga 2013)
Controlled experiments				
Common garden – I	1. Sampling of reproductive materials (rhizomes, seeds) from the field population across a disturbance gradient 2. Grow materials in a common environment 3. Sampling from plants grown in the controlled environment 4. Analysis with molecular markers and methylation sensitive restriction enzymes (Box 1) 5. Statistical analysis to identify epigenetic variation that is not explained by genetic variation	(Abratowska et al. 2012; Richards et al. 2012)	1. Minimization of epigenetic differences induced among sampling locations 2. Detection of stable and heritable (through clonal propagation) epigenetic changes (Bossdorf et al. 2008) 3. By controlling genetics and environment, quantification of epigenetic variation is possible	1. Experimental design may be narrow and therefore, may oversimplify the dynamic ecological factors existing in the wild populations (Spens and Douhovnikoff 2016) 2. Not suitable for outcrossing species as genetic identity of the field population is unknown
Common garden – II	1. Collection of known genotypes (e.g. from seed stocks, seeds from asexual variants of apomictic plants) 2. Exposure to environmental treatments 3. Seeds collected from treated plants and grown in control environment 4. Samples from controlled environment plants 5. Analysis with molecular markers and methylation sensitive restriction enzymes (Box 1)	(Bossdorf et al. 2010; Verhoeven et al. 2010)	1. Identification of stress induced DNA methylation patterns 2. Heritability of traits	Not suitable for sexually reproducing species in case the genetic variation is unknown and seed stock is not available
Natural population + Common garden	1. Genetic and epigenetic profiling (Box 1) from field sampled plant materials 2. Grow material in a common environment 3. Reciprocal transplantation of the plants grown in common environment 4. Sampling from the transplanted plants 5. Analysis with molecular markers and methylation sensitive restriction enzymes (Box 1) 6. Statistical analysis to identify epigenetic variation that is not explained by genetic variation	(Gao et al. 2010)	1. Identification of epigenetic changes at a temporal scale (a plant's life time) 2. Direction of epigenetic alteration (reversible)	Challenging for sexually reproducing plant species

Box 1. Methodologies for screening epigenetic variation in invasive plants.

Molecular markers with methylation sensitive restriction enzymes:

A standard Amplified Fragment Length Polymorphism (AFLP) process followed by methylation sensitive AFLP (MS-AFLP or MSAP). In MS-AFLP, pairs of methylation sensitive restriction enzymes (isoschizomers) have been used to survey cystine methylation at restriction sites spread across the investigated genomes. In AFLP, MseI and EcoRI have been used to digestion of DNA extracts whereas HpaII and MspI with EcoRI have been used in MS-AFLP. AFLP and MS-AFLP are usually applied in parallel to compare genetic and epigenetic structures of populations using statistical techniques. Unlike HPLC- and ELISA-based assays which determined the proportion of methylated cytosines across the entire genome, the MS-AFLP can distinguish between different genomic locations or contexts (CG, CHG, CHH) of cytosine methylation from the banding patterns: CpG methylated loci (bands present in EcoRI/MspI only); nonmethylated loci (bands present in both profiles); loci hemimethylated at the external C of the restriction site (bands present in EcoRI/HpaII only) and noninformative loci (bands absent in both profiles). This methodology has been successfully applied to screen epigenetic variation in both invasive species [e.g. *Alternanthera philoxeroides* (Gao et al. 2010); *Fallopia* sp. (Iacarella et al. 2015; Richards et al. 2012); *Phragmites australis* (Spens and Douhovnikoff 2016)] and non-invasive species [*Taraxacum officinale* (Verhoeven et al. 2010); *Viola elatior* (Catford et al. 2009; Roman and Darling 2007; Schulz et al. 2014)].

Although the commonly used pair of isoschizomers (HpaII/MspI) can identify changes in methylation pattern, they fail to support data concerning genetic variation exclusively. To circumvent this limitation, some authors suggested use of met-AFLP along with AFLP procedure. In met-AFLP, the restriction enzymes Acc65I/MseI and KpnI/MseI have been used. For example, Chwedorzewska and Bednarek (2012) used AFLP and met-AFLP to characterize genetic and epigenetic variation in invasive *Poa annua* population in Antarctica. In case of non-invasive species, Abratowska et al. (2012) used this procedure to identify genetic distinctiveness of metallicolous and non-metallicolous populations of a metallophyte, *Armeria maritima*.

Future directions:

Among the advanced and more powerful technologies, bisulfite sequencing-based methods are now being used for screening epigenetic variation (e.g. Schield et al. 2016; Spens and Douhovnikoff 2016; van Gurp et al. 2016). In these methods, unmethylated cytosines are converted to uracil, and methylated cytosines are identified by comparing a treated sample to a reference sample. Quantification of small (s) RNAs that influence de novo establishment and maintenance of DNA methylation at many sites may also provide insights into the heritable epigenetic variation in plants (see Bond and Baulcombe 2014).

grown in drought condition and increased growth of offspring ramets from the parents treated with repeated application of jasmonic acid. Application of 5-azacytidine to the parents exposed to the drought condition and application of jasmonic acid reduced the growth of maternal ramets (transplanted main stolon). These findings provide evidence that parental environment can induce transgenerational effects in the offspring and some of these effects can be adaptive.

Focusing on a specific gene methylation variation can also provide two important insights: in case of genetically uniform species, variation in gene or protein expression (measured using microarrays or 2-D electrophoresis) indicate underlying epigenetic variation (Bossdorf et al. 2008) and secondly, the expression of the methylated gene may highlight the mechanism by which methylation differentiation contributes to the successful invasion (Xie et al. 2015). For example, the C-repeat/dehydration-responsive element binding factor (CBF) pathway governs plant responses to adverse low temperature (Chinnusamy et al. 2003). Demethylated upregulation of cold response regulator *ICE1* (inducer of CBF expression 1) was found to be the evolutionary mechanism responsible for northward expansion of the invasive *Ageratina adenophora* (Crofton weed) in China (Xie et al. 2015). Use of Quantitative Trait Loci (QTL)-mapping approaches can be useful to link the natural epigenetic variation with the observed phenotype. QTLs have been recognized as genetic regions (associated with phenotypic traits) which control the magnitude of a specific trait (Cortijo et al. 2014). Epigenetic QTLs, or the loci associated with different methylation marks, have been found to control flowering time and root length in the model plant *Arabidopsis*, thereby demonstrating that heritability of some traits can be determined by epigenetic variation (Cortijo et al. 2014).

Finally, a higher degree of phenotypic plasticity in an invasive species does not necessarily mean that the species has become invasive due to the plasticity (Palacio-López et al. 2015). To infer the role of phenotypic plasticity in successful invasion, observations of trait plasticity should be followed by experimental studies to identify that the plastic response is adaptive or linked to fitness (Davidson et al. 2011; van Kleunen and Fischer 2005). Characterization of reaction norms of the study species (e.g. comparison between native and invasive lineages) grown in common garden in response to environmental gradients (marked '4' in Figure 2) may highlight the trade-offs between maintaining a high performance across a range of conditions (robustness or jack of all trades) and maximizing fitness in an environmental condition (opportunism or master of some) or both (robust to environmental conditions and high performance, the general purpose genotype) (e.g. Drown et al. 2011).

Concluding remarks

This review, being especially focused on plant invasion, has provided a comprehensive account of the molecular mechanisms of trait fitness of invasive plants. The strength of this review lies in the proposed framework that will encapsulate the ecological and evolutionary aspects of phenotypic variation. Future ecological stud-

ies should consider looking into the relative contributions of genetic variation and epigenetic modification to the observed phenotypic variation in invasive plant species, and characterizing the three-way relationship between environmental cue, phenotypic plasticity and epigenetic changes. This framework also suggests that these studies should combine trait and molecular data and include comparative analysis of fitness functions between native and introduced ranges of a species (van Kleunen et al. 2018) and explore adaptive differentiation in invaders, while accounting for non-adaptive evolutionary changes. The unified research framework, therefore, may converge the parallel lines of research towards a better understanding of the mechanism of successful invasion.

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